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A Computer Analysis of Relationships Between Orders of Chrysophyta

DAVID P. OLDS*

ABSTRACT — The division Chrysophyta has previously been formulated to include three diverse groups. A computer analysis was made of the individual orders within the division to determine the "naturalness" of this grouping and also to show how computer techniques may be used for this purpose. The computer methods are described, and a possible system of classification of the division based on the computer analysis is presented.

The division Chrysophyta was first proposed by Pascher in 1914 (cf., Papenfuss, 1955) to include the yellow-green algae or Xanthophyceae, the golden-brown algae or Chrysophyceae, and the diatoms or Bacillariophyceae. Previous to that time, the Xanthophyceae were often grouped with the Chlorophyceae; the Chrysophyceae were placed with the Flagellatae; and the Bacillariophyceae were thought to be distantly related to the Phaeophyceae. Phycologists have now generally agreed on the relationship between the Xanthophyceae and the Chrysophyceae. However, there is some disagreement on the closeness of the Bacillariophyceae to the other Chrysophyta; most workers have considered the diatoms to be somewhat more distantly related to the Xanthophyceae and to the Chrysophyceae than these are to each other. The history of classification within this group has been reviewed in detail by Papenfuss, (1955), Smith, (1955), and Fritsch, (1951).

The characteristics which unite these groups have been found in various combinations throughout the division to afford considerable evidence of their affinity with each other. The most important features that the groups have in common include:

- 1) The stored food reserves including fats, oils, and leucosin in many members, and the lack of starch in all members.
- 2) similarities in pigmentation, both in kind and relative abundance.
- 3) the cell wall, when present, basically composed of pectin and frequently consisting of two pieces.
- 4) the formation of a distinctive type of asexual reproductive structure, the statospore, in many members of the division.

Objectives of this study were to determine the degree of similarity between the three groups of Chrysophyta as previously delimited to see if they constituted a "natural" grouping, and to illustrate how computer methods may be used for this type of analysis.

The broadest conception of Chrysophyta was adopted so that it would be possible to test the appropriateness of grouping all the orders under the heading Chrysophyta. In other words, should this division continue to stand, or is it artificial and is realignment necessary?

The orders for this study are described in Smith's *Cryptogamic Botany* (1955), *Botanique* (Feldman, 1963), and *Engler's Syllabus* (Krieger, 1954). These and

other sources gave sufficient information to characterize the 13 orders listed in Table 1. Parallel data were then assembled for a series of 59 characteristics (Table 2) for each taxon (Table 1) and scored + (plus) or - (minus) for presence or absence of that characteristic within the order (Table 1). The governing principal on how to score the taxon was that of primitiveness of the *character* concerned. It was assumed that certain phyletic sequences such as those given in *Engler's Syllabus* are acceptable, so that it was possible to determine the most primitive characters in each order. This must be clearly distinguished from the unrelated question of which organism in each taxon is the most primitive. In this way the degree of similarity between the orders could be determined without the intentional weighting of the data other than the unavoidable subjectivity inherent in the acceptance of any set of phyletic dicta such as those referred to in Table 3.

These data were then analyzed by a method developed by Orloci (1967) called 'optimal agglomeration.' This is a clustering method operating on the 'within group sum of squares' as the agglomerative criterion. By *clustering method* is meant a procedure, carried out by the computer is this instance, which reviews the data from Table 1 (presented to it through the medium of punch cards) and resolves the data in such a way that successive pairs of most similar taxa are grouped. By *within group sum of squares* is meant the total of the squares of the "distance" between each pair of characteristics being compared taxon by taxon. By *agglomerative criterion* is meant the method by which these within-group sums of squares are grouped or clustered. Agglomeration is carried out by the computer in successive cycles, each cycle minimizing the within-group sum of squares and maximizing the differences between groups or taxa. The outcome is a set of values that permits the computer to determine which taxa are most similar. The graphic visualization of these data derived from Orloci's optimal agglomeration analysis is the dendrogram shown in Figure 1.

Calculation of the relationships of the groups for construction of this dendrogram starts by examining the final clustering cycle for its average within-group dispersion. This value establishes the 100 per cent dispersion level. Each successive clustering cycle preceding this final one is then examined to determine which orders were clustered and how far apart they were as a percentage of the 100 per cent dispersion level. After all the clustering cycles have been calculated, a dendrogram is drawn using the dispersion levels (Fig. 1).

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TABLE 1. Orders of Chrysophyta scored for presence (1) or absence (0) of each characteristic.

Order	Characteristics 1-59
A Heterochloridales ..	0000101010011100011010100010011001001000000000010000100001
B Rhizochloridales ...	0000101010011100011011100000000011001000000000010000000001
C Heterocapsales	00001010100111000100100100110010000101000100010000000000001
D Heterococcales	11100010100111000111111000000010000001000000000000000100001
E Heterotrichales	11110010100111000110100011100010000001110100110000000000001
F Heterosiphonales ..	00000010100011000111011000000100000101110100110000000010011
G Chrysomonadales ..	00001001010101010100101000001011000010110100001000000100011
H Rhizochrysidales ...	00001001010100110110101100000001010010000000001100000100010
I Chrysocapsales	00001001010100110100100111100001000010000000001000000000001
J Chrysosphaerales ...	10100001010100110110101100100001000010000000101000000100001
K Chrysotrichales	00001001010100110100100111100010000010000000001000000000001
L Centrales	11100101001011011011101000010000101110110010101001011001000
M Pennales	11100101001100111111101000010000101001111101001101111000100

The dendrogram shows the relationship of each order to the order that it most closely resembles. Levels of relationship are shown as per cent of within-group dispersion as it relates to the 100 per cent dispersion of the most distantly related group. For example, *Heterochloridales* and *Rhizochloridales* are most closely related to each other, this being at 14 per cent dispersion. This method can show how the total of these two groups is related to the next closest group but not how each individual order is related to each other order.

The outstanding weakness of this method of presenting phyletic materials is clear. The dendrograms (actually, the computer-generated data) relates taxa in *pairs*. This can hardly be considered an unbiased presentation of the relationship — nevertheless it has certain advantages, such as the use of per cent of within group dispersion for the tentative establishment of taxa higher than the ordinal level.

The objections to the above approach for determining the degrees of similarity between taxa are met, at least in part, by the method called "principal components analysis," also developed by Orloci (1966). This method plots the locations of each of the orders in multi-dimensional space, giving successive values for their statistical separation. Unlike the optimal agglomeration analysis, this method allows a calculation of the relationship of each individual order with every other order.

The results of the analysis for the first three axes are shown in Figure 2. These axes give an accumulative efficiency of 64 per cent of the total efficiency of the relationships of the orders in the multi-dimensional space. Adding additional axes does not give a great increase in efficiency for any single axis added after the first three. The results show the separation of the same three major groups found with the optimal agglomeration analysis. However, there appears to be some realignment within and among these groups. For instance, orders D and E are shown to be most closely related to each other in the optimal agglomeration analysis, while in the principal components analysis order D is more closely related to order F than it is to order E. The principal components analysis also shows that the group of points constituting the Chrysophyceae is more closely related to the Xanthophyceae than to the Bacillariophyceae; the optimal agglomeration analysis had placed the Chrysophyceae closer to the Bacillariophyceae than to the Xanthophyceae.

These analytical methods show close correlation with the classification schemes formulated in the literature; however, in addition to the three classes generally agreed upon, a grouping a subclasses might give greater clarity to the relationships between the orders. Using the coordinates of each order obtained from the principal components analysis, the distance between the orders can be calculated. These distances give a clear separation of nine groups which could be considered subclasses (Table 4).

Statistical analyses of this sort have the advantage of easy graphic presentation. A dendrogram or a three-dimensional model may be able to convey the multitude of diverse relationships among many groups much better than the written word. This type of analysis also has the

TABLE 2. Characteristics used for the computer analysis.

1. Silicified cell wall	28. Dendritic colony
2. Pectic cell wall	29. Flagella, 2, equal, apical
3. 2 articulated cell walls	30. Flagella, 2, unequal, lateral
4. H-shaped wall structure	31. Flagella, 2, unequal, apical
5. Naked cells	32. Flagellum, 1, apical
6. Chlorophyll c	33. Non flagellated
7. Chlorophyll e	34. Amoeboid vegetative cells
8. Fucoxanthin	35. Auxospores produced
9. Heteroxanthin	36. Zoospores produced
10. Lutein	37. Statospores produced
11. Diatoxanthin, etc.	38. Aplanospores produced
12. Chromatophores, one or two	39. Sexual reproduction
13. Chromatophores, many	40. One zygote formed
14. Chromatophores, mostly disc	41. Two zygotes formed
15. Not above	42. Isogamous
16. Leucosin	43. Oogamous
17. Volutin	44. Amoeboid motile gametes
18. Fresh water	45. Flagellated motile gametes
19. Marine	46. Haploid life cycle
20. Terrestrial	47. Diploid life cycle
21. Uninucleate vegetative cells	48. Protoplasmic streaming
22. Multinucleate vegetative cells	49. Phagotropic nutrition
23. Unicellular vegetative soma	50. Girdle band
24. Colonial vegetative soma	51. Raphe
25. Filamentous vegetative soma	52. Punctae
26. Branched filaments	53. Costae
27. Palmelloid or gelatinous colony	54. Veg. contractile vacuole
	55. Siphonaceous
	56. Radial symmetry
	57. Bilateral symmetry
	58. Rhizopodal
	59. Sessile

TABLE 3. Assumed phyletic sequences for determining primitiveness of the characteristics.

Primitive → Advanced
1. Wall pectic → naked protoplast
2. Complete wall → H-shaped wall → 2 articulated cell walls
3. Unicellular soma → colonial soma
4. Unicellular soma → simple filament → branched filament
5. Uninucleate cells → multinucleate cells
6. Flagella → non flagellated
7. 2 flagella → 1 flagella
8. Isogamous → oogamous
9. Many chromatophores → one chromatophore

advantage of being impartial; no one characteristic being weighted more than any other. However, some biases may unintentionally be present. Bias could result from having greater numbers of characters in a particular area of investigation, such as pigment types. Most of the characters used for this analysis were morphological because most of those found in the literature were morphological. Unfortunately, comparative biochemistry and comparative cytology have failed to provide data for each of the orders of Chrysophyta. Therefore, available information could not be used for any of the orders. There is also the philosophical bias present due to the interpretation of phyletic sequences. Of necessity, the analysis presented here must be taken as provisional in its taxonomic implications and conclusions.

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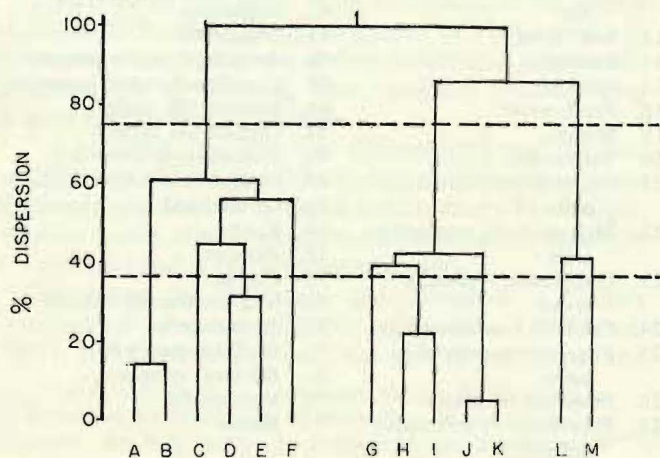


FIGURE 1

TABLE 4. A possible classification scheme of subclasses using data from the principal components analysis.

Order	Subclass	Class
Heterochloridales	Heterochlorididae	Xanthophyceae
Rhizochloridales		
Heterocapsales	Heterocapsidae	Xanthophyceae
Heterotrichales	Heterotrichidae	Xanthophyceae
Heterococcales	Heterosiphonidae	Xanthophyceae
Heterosiphonales		
Chrysomonadales	Chrysomonadidae	Chrysophyceae
Chrysocapsales		
Rhizochrysidales	Rhizochrysididae	Chrysophyceae
Chrysosphaerales	Chrysotrichidae	Chrysophyceae
Chrysotrichales		
Centrales	Centridae	Bacillariophyceae
Pennales	Pennidae	Bacillariophyceae

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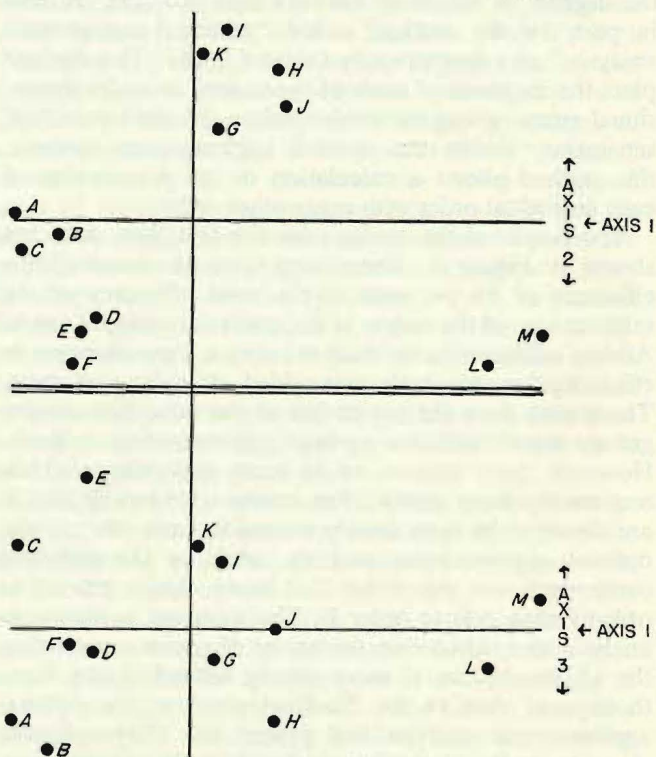


FIGURE 2